Cochlear Vibrations in Response to Swept-tone Stimulus

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Abstract. Perceptually, tones that rapidly sweep up in frequency (up-sweeps) tend to be better maskers than tones swept downward (down-sweeps). It has been hypothesized that this sensitivity to sweep direction stems from the dispersive properties of the cochlear traveling wave. Our previous mouse-based research supports this hypothesis: At the 9-kHz tonotopic location, cochlear vibrations were more strongly suppressed by up-frequency-sweep suppressors compared to down-sweep ones when the rate of frequency change approached the rate of cochlear dispersion. However, when the sweep rate was slow relative to dispersion, sweep direction (i.e., up vs. down) did not affect suppression strength. Human behavioral and otoacoustic emission experiments utilizing similar stimuli revealed that the difference in masking/suppression strength between up- and down-sweeps varied systematically with sweep rate. Sweep direction had a significant effect when the sweep rate approximated the estimated human traveling wave velocity but was insignificant for slower and faster rates. In this study, we aim to determine whether similar behavior is observed in cochlear vibration suppression for sweep rates exceeding cochlear dispersion rate in mice. The estimated human cochlear dispersion rate (~0.5-0.1 oct/ms) is considerably slower than observed velocities in mouse intracochlear vibrations (~1.8 oct/ms). This presents a practical challenge when generating sweeps with rates matching or exceeding rodent dispersion rates, potentially introducing acoustic distortions at stimulus onset/offset. To address this, we devised a sweep where instantaneous frequency varies with time following a sigmoid function, allowing for gradual envelope tapering without affecting mid frequencies even at exceptionally fast sweep rates (~50 oct/ms). With this novel sweep design, we demonstrated that the difference between up and down-swept suppressors depends on sweep rate, following a bell-shaped pattern, with maximal sensitivity to sweep direction occurring at or above the rate of cochlear dispersion in mice. These results demonstrate that cochlear dispersion, although passive phenomenon itself, can shape nonlinear processing of dynamic sounds.

INTRODUCTION

Ecologically relevant sounds, such as speech, birdsongs, echolocation calls, possess a complex structure in terms of their spectro-temporal characteristics. However, cochlear processing is often studied using simple sounds like pure tones or clicks [1]. Despite the polar differences in their temporal properties, these stimuli elicit surprisingly similar cochlear responses, leading to the representation of cochlear processing by static linear bandpass filters that ignore the temporal fine structure of sound [2],[3]. Nevertheless, such filterbank models fail to predict the cochlea's handling of dynamic sounds, even relatively simple ones like closely spaced clicks [4]. Thus, to better understand how sounds with complex spectro-temporal features, such as formant transitions, are processed, we need to have a better understanding of how the cochlea, the first stage of the auditory processing pathway, codes them.

Classic psychoacoustic studies utilizing frequency sweeps, known as Schroeder harmonic complexes, exemplify the auditory system's sensitivity to stimulus temporal fine structure [5]. Specifically, upward sweeps, where instantaneous frequency increases over time, are much more efficient maskers of tonal signals compared to their time-reversed counterparts, downsweeps [6],[7]. This masking sensitivity to sweep direction has been attributed to cochlear dispersion, which manifests itself as an upward frequency glide in cochlear impulse response [2],[8],[9]. (Note: at the apex, the direction of the glide appears to be reversed, as inferred from the recordings from auditory nerve responses [10]–[12].) Thus, the upward sweep stimulus enhances local cochlear dispersion, resulting in responses that ring longer, while the downward sweep counteracts it, resulting in more time-compressed responses. Direct measurements of basilar membrane (BM) vibrations confirm this general pattern [2],[8],[13]. While cochlear

glide and dispersion are considered passive phenomena, the sensitivity of BM suppression to sweep direction suggests that cochlear dispersion modifies the active processing of concurrent sounds [2],[13]. Behavioral studies support this hypothesis, as the masking sensitivity to sweep direction decreases at higher stimulus levels and in hearing impaired subjects [14]. Furthermore, human data suggest a strong dependence of up-down masking differences on sweep rates, with a general pattern of decreased differences at faster sweep rates [6],[7]. In contrast, in mice, the difference in up/down sweep efficiency increased with increasing the sweep rate towards the rate of dispersion at ~9 kHz location (~1.3-1.8 oct/ms) [3],[13]. We hypothesize that this species differences relate to differences in the rate of cochlear dispersion, rather than differences in cochlear processing. Thus, the largest sensitivity to sweep direction should occur when the temporal properties of the suppressor/masker match the rate of cochlear dispersion in given species/cochlear location. Our behavioral and otoacoustic emission data in humans corroborate the prediction that masking/suppression differences are indeed nonmonotonic and bell-shaped in function of sweep rate (see [15] in this volume).

The aim of this study is to investigate suppression sensitivity to sweep direction directly in cochlear vibrations in mice across a wide range of sweep rates, designed to span ranges that are both considerably slower and faster than the rate of cochlear dispersion. We have designed a special sweep stimulus, the sigmoidal sweep (Fig. 1), which, unlike exponential or linear sweeps, allows obtaining fast sweep rates within a finite time window without producing acoustic distortions at the stimulus onset/offset. We extend our previous study by including measurements from the tectorial membrane (TM) overlying the organ of Corti, in addition to recordings from the BM [13]. Because the TM directly overlies the inner hair cell stereociliary bundles, its motions may provide the most accurate characterization of the stimulus shaping the afferent auditory response [16]. Importantly, motions of the organ of Corti and TM do not simply follow the motions of the BM but demonstrate a wider dynamic range, extended regions of amplification, and two-tone interactions [17],[18]. Thus, characterizing how temporal processing varies within these structures may provide a better understanding of how frequency sweeps are processed in the cochlea, and how these processes shape perception (e.g., up-vs-down behavioral masking).

METHODS

Experiments were conducted in deeply anesthetized (ketamine and xylazine) adult mice (CBA/CaJ; n = 9). The animal preparation and instrumentation is described in details elsewhere [3]. In short, the left pinna was resected and a tip of a ER10X OAE probe assembly (Interacoustics, Denmark) was sealed to the remaining ear canal. The bulla was opened to expose the otic capsule for vibrometry measurements from the apical turn of the cochlea, corresponding to ~8–9 kHz tonotopic location. The vibrometry was performed with a custom-built volumetric optical coherence tomography and vibrometry (VOCTV) system (100-kHz sampling rate). The laser light was focused near either basilar membrane (BM; n = 7) and/or tectorial membrane (TM; n = 4).

The acoustical stimuli were designed digitally (100-kHz sampling rate) and consisted of pure tones and swept tones. Slow 40-dB SPL exponential sweeps were used to identify characteristic frequency (CF) [3]. For suppression experiments the stimuli were presented in three-buffer configuration: probe alone, probe plus suppressor sweep, and probe plus suppressor with inverted polarity. Each buffer duration was set to be 100 ms or its whole division, with shortest buffer set at 5 ms for the most rapid sweeps. All buffers were presented with 4-ms interbuffer gap discarded in the analyses. The responses were averaged from 200 to 4000 times to get at least an equivalent of 20 s recording time per buffer. The sweep duration was set to the buffer duration, including 2-ms onset/offset cosine ramps. The duration of the tone was extended by 1-ms at each end effectively reducing the interbuffer gaps to 2 ms. Tones were

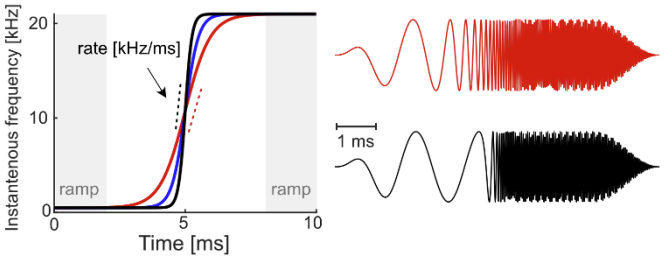

FIGURE 1. Sigmoidal sweep stimuli design. Instantaneous frequency of the sweep was modeled after a sigmoid function (left panel) to obtain a specific sweep rate c [kHz/ms] at the center frequency and half-time. Examples of the corresponding time-waveforms are shown on the right. By using a sigmoid function to generate the sweep stimulus, it become possible to taper the onset/offset of the stimulus (gray bands) without affecting the energy at frequencies around the center frequency.

ramped with 2-ms cosine window. The phase of the tone was either pseudorandom relative to the suppressor sweep (but fixed within the test condition) in one group of animals (n = 5) or set to be in phase with the closest frequency component of the sweep in another group (n = 4). In three mice from the latter group, the phase of the tone was varied to be either in or out of phase with the closest sweep component for a subset of the tested rates. We observed that the tone phase did not affect the amount of suppression seen at the probe frequency. Thus, the data from both groups are presented together. The probe frequency was set at CF and level of 40 dB SPL. The sweep frequency was varied within 0.5 to 20.5 kHz range, with instantaneous frequency level set at 60 dB SPL. The instantaneous frequency of suppressor sweep modeled following a sigmoid function:

$$f(t) = f_1 + \frac{f_2}{1 + e^{c(t_{1/2} - t)}}, \quad (1)$$

where f_1 and f_2 are sweep's lowest and highest frequency, respectively, and c is the slope of the function at half time, $t_{1/2}$. The f(t) function was then converted to a sweep waveform as described in [19]. All sweeps were generated as upward sweeps, and time reversed to obtain a corresponding downward sweep. We utilized a sigmoidal sweep instead of an exponential one, as it allowed to generate waveforms with fast sweep rates within a finite time window. For comparison, the sigmoidal sweep rate c [kHz/ms] was converted to an equivalent exponential sweep rate r [octaves/ms] at the probe frequency, f_p as:

$$r(f_p) = \frac{c}{\ln(2)\, f_p}. \quad (2)$$

Across the presentations the sweep rate was varied from ~0.1 to ~50 oct/ms in equal steps on a logarithmic scale. The order of presentation of was randomized, but with upward/downward sweep conditions of same rate presented in an interleaved fashion. The suppression residual waveform was calculated as difference between cochlear response to the probe alone *vs*. probe plus suppressor conditions, as described in [4],[20]. The suppression residual magnitude was evaluated at the frequency of the probe tone in the frequency domain (via FFT). The difference in the suppression residual magnitudes between up/down sweeps (in dB) was calculated only if the corresponding responses to a probe-alone buffer at f_p were less than 2 dB apart.

At the end of the experiment the animals were euthanized, and some tests were repeated *post-mortem*. All procedures were approved by the Institutional Animal Care and Use Committee at USC.

RESULTS

Figure 2 summarizes the effect of sweep direction on the suppression of cochlear response to a low-level CF-tone (individual data points represented by circles, with a trend line in red). A line at 0 dB would indicate no effect of sweep direction on suppression of tonal response; positive/negative values indicate that upsweeps/downsweeps were more efficient suppressors, respectively. Consistent with our previous study utilizing exponential sweeps [13], upsweeps become more efficient suppressors compared to downsweeps as sweep rates increase towards the rate of cochlear dispersion (i.e., the slope of the frequency glide in the cochlear impulse response; gray band) [3]. However, testing a wider range of rates with sigmoidal sweeps reveals a nonmonotonic and bell-shaped pattern of suppression

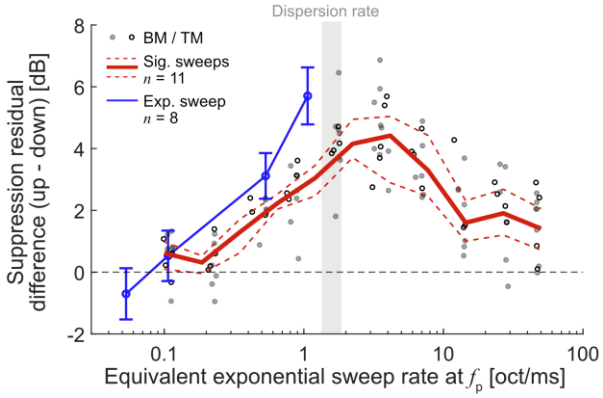

FIGURE 2. The effect of sweep direction on suppression of the probe tone response at BM (n = 7; gray circles) and/or TM (n = 4; open black circles). A loess trend line (solid) with ±95 confidence intervals (CIs; dashed) is shown in red. The CIs were calculated via bootstrapping blocked by an animal ID. Mean data (±95% CIs) for suppression difference caused by exponential frequency sweeps of opposing directions are shown in blue (n = 8; adapted from **[13]**).

sensitivity to sweep direction. Upsweeps are more efficient suppressors than downsweeps only when sweep rates are close to the natural dispersion rate of the cochlea. At slower and faster sweep rates, the differences are close to 0 dB, indicating that both up and downsweeps were equally efficient.

The same pattern of up/down suppression differences is observed for both BM and TM vibrations at least when just the residual magnitude is considered. While the suppression residuals as well as responses to a probe tone were typically larger for TM vibrations compared to BM (by ~5-10 dB), the effect of sweep direction was similar in magnitude. Therefore, data for both TM and BM motions were included in Fig. 2.

To better understand the reasons behind the differences in up/downsweep suppression efficiency, we examined the cochlear response to suppressor sweeps themselves. When the sweep rates were considerably slower than the dispersion rate, the cochlear vibrations in response to sweeps of opposing directions were time-reversed versions of each other, as previously shown [13]. For sweeps presented at considerably faster rates, the cochlear responses to both up and downsweeps were similar and resembled response to a click stimulus (not shown). However, when the sweep rate was within the range of cochlear dispersion, differences between up/downsweep responses emerged: the upsweeps produced longer-lasting responses, while downsweeps produced peakier and time-compressed responses (see Fig. 3, top panels). Consequently, the upsweep suppressed the tonal response for a longer time period compared to the downsweep (middle panels), as also evidenced by the suppression residual responses (bottom). Thus, despite being a passive phenomenon, cochlear dispersion can modify the nonlinear processing in the cochlea.

DISCUSSION

The aim of this study was to investigate the suppression of cochlear responses to tones by sounds with varying temporal properties, specifically frequency sweeps. Behaviorally, sweeps can significantly impact the masking of pure tones, with the direction of frequency change influencing masking effectiveness, with upsweeps being more efficient maskers (by up to 20 dB) than downsweeps [6],[7],[14]. Given that ecologically relevant sounds often exhibit dynamic characteristics, including variations of frequency sweeps (e.g., formant transitions, tonal languages, echolocation, bird songs), understanding the mechanisms underlying the auditory system's sensitivity to temporal fine structure, such as the direction of frequency change in sweep sounds, is crucial. While sensitivity to temporal fine structure may develop across several stages of the auditory processing pathway, this study focuses on examining it at the level of the cochlea. We hypothesize that cochlear dispersion and its effects on nonlinear processing are the underlying mechanisms driving this phenomenon. This hypothesis was tested by measuring cochlear suppression of a low-level CF-tone by up/down sweeps of varying rates, covering a range below and above the rate of cochlear suppression at the recording location in mice (~1.3-1.8 oct/ms). To achieve very fast sweeps

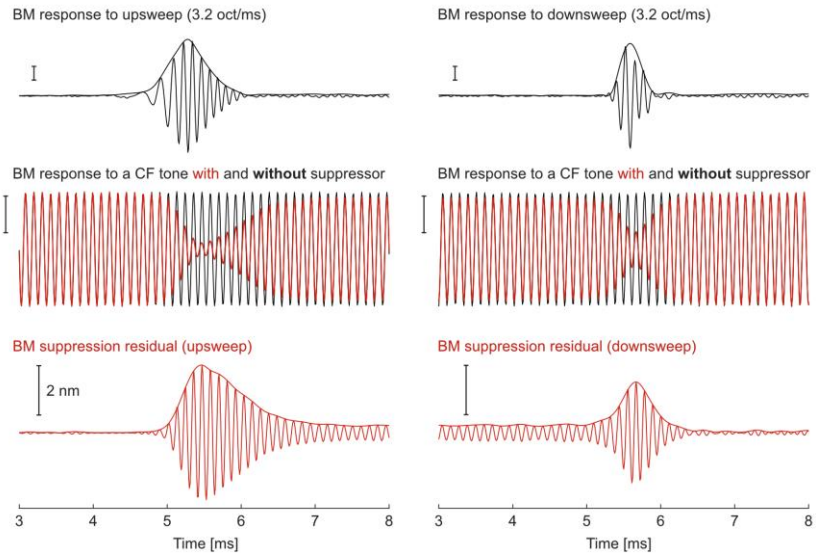

FIGURE 3. BM vibrations in response to sigmoidal sweeps (r = 3.2 oct/ms) and/or CF tones. The uppermost panel show the BM vibrations in response to upward (left) and downward (right) sigmoidal sweeps. The middle panels show the corresponding BM vibrations in response to CF-tone presented in isolation (black) or in presence of the suppressor sweep (red). In the bottom panels the corresponding suppression residual waveforms are shown (ID 040924; CF 8.8 kHz).

(~50 oct/ms), we devised sweeps where instantaneous frequency changes with time following a sigmoid function (Fig. 1), instead of using exponential or linear sweeps (e.g., Schroeder complexes). We predict that if cochlear dispersion influences suppression sensitivity to stimulus temporal fine structure, significant differences between up/down sweep suppression will only be observed when sweep rates are comparable to the dispersion rate. For sweep rates slower than the dispersion rate, the sweep stimuli are processed more like steady-state tones, while at significantly faster rates, they are processed more like clicks. Our results support this hypothesis, as indicated by a bell-shaped pattern of up/down suppression differences shown in Fig. 2.

Our results reveal that the effectiveness of suppression depends on sweep direction, with upward sweeps being more efficient suppressors than their time-reversed counterparts. This difference seems to be related to how the cochlea responds to the sweeps—upward sweeps evoke longer-lasting responses in cochlear vibrations compared to downsweeps (see Fig. 3, top panels). These differences occur only when the sweep rates are comparable to the cochlear dispersion rate at the recording location (between ~1-4 oct/ms) [3]. Similar qualitative differences in temporal properties of BM responses to sweeps of opposing directions have been reported previously in guinea pigs (at 17 kHz) and chinchillas (8 kHz) with periodic linear sweeps (Schroeder complexes) but presented at slower rates (~0.35 oct/ms and ~0.7 oct/ms, respectively) [2],[8]. The upward frequency glide appears to be a universal feature of a mammalian cochlea at the base, with the glide slope (i.e., dispersion rate) similar across common lab species when the time is expressed in units of CF periods rather than milliseconds, averaging to ~0.2 octaves/CF cycles across species [9]. This relationship extends to mice, predicting glide rate at 9 kHz place of 1.8 oct/ms—in agreement with direct measurements (gray band in Fig. 2). For guinea pig and chinchilla cochleae at 17 and 8 kHz locations, the maximal effect of the sweep direction on cochlear responses is predicted to occur at rates equivalent to ~3.4 and ~1.6 oct/ms or higher, respectively, thus at rates faster than previously tested. Future research should address this gap in literature.

We did not observe significant differences in sweep-direction sensitivity between TM and BM suppression (Fig. 2, open vs. closed circles). This suggests that suppression sensitivity to temporal fine structure is driven by the same mechanism, namely, global cochlear glide, rather than features specific to a particular structure, such as micromechanical resonances or vibrational modes within the organ of Corti [9],[21],[22]. However, our data cannot rule out the existence of additional vibrational modes that may globally affect the glide.

Our data support the hypothesis that cochlear dispersion can affect nonlinear processing of dynamic sounds, contributing to the sensitivity of the auditory system to temporal fine structure. This interpretation is consistent with decreased sensitivity to temporal fine structure in hearing impaired subjects as well as at higher intensities, as seen in behavioral responses, neural firing rates and cochlear vibrations [2],[14],[23]. Furthermore, neural data indicate that sweep direction discrimination persists in spike rates at least up to the level of the inferior colliculus [24]–[26]. For instance, cochlear implant users can discriminate between up/down sweeps relatively well, suggesting that the order of electrode excitation (low to high vs. high to low) is a sufficient clue [27]. Whether these subjects experience similar sensitivity to sweep direction in masking experiments remains unknown. Furthermore, birds can discriminate between up/down sweeps, but when masking is evaluated, the effect of sweep direction is minuscule [24],[28],[29]. This is an interesting observation, as avian basilar papilla appears to support dispersive traveling waves, but thus far, there is no evidence for these motions to be amplified as in the mammalian cochlea [30]–[33].

Altogether, these reports are consistent with our interpretation that both cochlear dispersion and nonlinear amplification are needed to produce masking differences by sweeps of opposing directions, as previously demonstrated for click-on-click suppression [4]. These data reveal that many aspects of temporal processing in the cochlea remain to be characterized. Further research in this area will contribute to a deeper understanding of auditory perception and processing of dynamic sounds.

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COMMENTS AND DISCUSSION

[**Sebastiaan Meenderink**]: Thanks for your wonderful chapter. Per usual, I find your observations fascinating, they trigger many questions in my mind. Is it correct for me to assume that dispersion rate varies both with cochlear location (CF) and the frequency bandwidth over which you calculate this? If so, what did you use for the latter? Frequencies around CF?

[**Karolina Charaziak**]: Thank you, for thoughtful comments! You are correct to assume that dispersion rate varies with CF, when expressed in units not normalized to CF, such as kHz/ms. When expressed in units normalized to CF, such as octaves/CF cycle, the dispersion rate is roughly independent of CF (at least for "basal" end of the cochlea). Because the instantaneous frequency glide becomes shallower when frequency approaches CF, it is important to consider the time window over which you calculate the slope (i.e., dispersion rate). I chose to calculate the slope over the steepest part of the glide, corresponding to the time window spanning range of 1.5 to 2.5 CF periods (see [3] for details).

[**Sebastiaan Meenderink**]: For Fig. 2, can you explain how the amplitudes of the "suppression residuals" are calculated? Is it the RMS of the (entire) residual waveform, or perhaps peak amplitude of the envelope? I can imagine that this definition has an effect on the "bell-shape" curve shown in Fig. 2.

[**Karolina Charaziak**]: In the Methods we define the residual magnitude as follows: "The suppression residual magnitude was evaluated at the frequency of the probe tone in the frequency domain (via FFT)." I chose this metric as we used the same calculation for evaluating SFOAE suppression in humans (see Salloom et al, in this volume). I

have also calculated the residual envelope duration as a metric of the suppression "strength" and it shows the same bell-shaped pattern. The peak amplitude of the envelope is not a good metric, as it only reflects on peak suppression.

[**Sebastiaan Meenderink**]: Figure 3: In your recent JASA paper (ref [3] in your MoH manuscript) you show that the frequency response curves are independent of sweep direction. Here, (Fig. 3 top two traces) I am not sure that is the case. In particular, the group delay for the upsweep seems shorter than for the downsweep. Is this correct? (or did the BM upsweep response get inadvertently shifted to the left a little bit?) I'm saying this, because I notice that for the upsweep, suppression seems "delayed" re. the BM sweep response. This could mean that suppressor freqs>CF are better suppressors. But this is not obvious for the downsweep paradigm. Perhaps it would be possible to extract instantaneous frequency from the BM sweep response and plot that against the envelope of the residual to see if there is frequency tuning in suppression?

[**Karolina Charaziak**]: These are great observations! In our JASA paper [3] we make a point that the BM transfer functions/impulse responses [i.e., normalized to the stimulus) do not depend on the sweep rate. Here we plot raw BM displacement, that is NOT corrected for stimulus delays, thus there are differences in the vibrations. If I plot the same data normalized to the stimulus, there is no difference between up/downsweep impulse responses (except the "ringing" part, but that is minor). You are right regarding the high-frequencies being better suppressors for up vs down sweeps – a paper on that coming soon!

[**Sebastiaan Meenderink**]: In our lab (gerbil, CF~25 kHz) we find that the response phase of a near-CF probe tone changes ~0.1 cycle with the introduction of a suppressor tone. The amount of phase change is independent of suppressor frequency. Do you see a similar effect in your data? (i.e., the unsuppressed (black) and suppressed (red) curves in Fig. 3, middle would have a small horizontal offset, but this is hard to see in the figure).

[**Karolina Charaziak**]: I do see a small phase effect as well, but I am hesitant to say whether it is frequency independent (it appears to depend on frequency for suppressors above CF). Again, a more detailed paper on these effects is in the workings!

[**Sebastiaan Meenderink**]: Figure 2, caption: "via bootstrapping blocked by an animal ID". I have no idea what this means. Initially I thought that the animal ID somehow prevented ("blocked") the bootstrap method, but I assume it refers to some form of grouping of the responses?

[**Karolina Charaziak**]: In general, you do not do bootstrapping on repeated measures, but if you resample by selecting from IDs you can correct for some repeated measures (i.e., you are resampling not individual points, but groups of data coming from a common animal).

[**Sarah Verhulst**]: Very nice talk. People use sweeps to get better ABR responses, so I am wondering if in mice you need to use different sweeps than in humans to get peakier ABR responses?

[**Karolina Charaziak**]: I think this is all relative to which region or which frequency you are testing, so if you express your sweep in relative units it is going to be similar, but if you express it in kHz/ms it is going to vary vastly between frequency you want to assess, ABR, so you do want to think about the species.

[**Christopher Bergevin**]: Sorry if you said this, since with OCT you have some special resolution, do the glide response varies across different locations, throughout the organ of Corti,

[**Karolina Charaziak**]: In this case I studied tectorial membrane and basilar membrane, and I didn't see many differences, so to the gross approximation the answer is no. The way I analyze the data they look similar, but the devil is in the details, which I did not show, and there are some differences in suppression characteristics, mostly because in the organ of Corti and TM we see nonlinearity spreading to much lower frequencies, which is not seen in the BM, so when you analyze frequency by frequency you will see differences there, but not at the global level.